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Cytogenetic Differentiation, Geographic Distribution, and Domestication in Palearctic Sheep (*Ovis*)

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Many authors have contributed to the taxonomy of Palearctic sheep of the mouflon-urial-arkhar/argali types (SEVERTSOV 1873a, b; LYDEKKER 1898, 1912, 1913; NASONOV 1911, 1923; TSALKIN 1951; SOKOLOV 1959; HEPTNER et al. 1961). The existing taxonomic systems were reviewed in detail by TSALKIN (1951); Table 1 summarizes the number of species and subspecies recognized by different authors. Within

Table 1
Variations in the number of taxa within Palearctic *Ovis*

Author Number of taxa	Severtsov (1873a)	Lydekker (1898)	Lydekker (1913)	Nasonov (1923)	Tsalkin (1951)	Ellerman und Morrison Scott (1951)	Sokolov (1959)	Heptner (1961)	Haltenorth (1963)	Pfeffer (1967)
Genera and subgenera	2	1	1	1	1	2	2	1	1	1
Species	17	8	6	9	2	5	4	2	1	1
plus Subspecies	—	17	26	37	28	37	35	23	37	8

the Palearctic, SOKOLOV (1959) recognized three species (*O. musimon*, *O. orientalis*, *O. ammon*) while TSALKIN (1951), HEPTNER et al. (1961) and PFEFFER (1967) considered all sheep between the Mediterranean and eastern Mongolia assignable to *Ovis ammon*. All authors regarded the snow sheep of eastern Siberia, which is geographically isolated from *O. ammon* s. str., as a distinct species to which either the names *O. nivicola* or *O. canadensis* were applied.

The number of recognized species within the mouflon-urial-argali group of sheep reflects a change in taxonomic thought regarding the species concept, which ranges from a very narrow view (NASONOV 1923; LYDEKKER 1913) to a very broad species concept (HALTENORTH 1963). Moreover, acceptance of mouflon and argali types of sheep as one species resulted in the recognition of a polycentric process in sheep domestication (BOGOLYUBSKII 1959; ZEUNER 1962) which, in turn, led to corresponding historical conclusions.

BUTARIN working in LUS' laboratory was the first to compare the chromosome complements of wild arkhar/argali sheep from the Tyan-Shan with domestic sheep (1935 a, b). Early cytological techniques only permitted BUTARIN to establish chromosome numbers in single metaphase plates; figures of those metaphase plates adequately represent the correct $2n = 56$ in *O. polii karelini*, and $2n = 54$ in fat-tailed sheep, *O. aries steatopyga* (BUTARIN 1935a:79, figs. 1, 2). Inexplicably however, BUTARIN assigned 60 chromosomes to them and gave this number in his subsequent work (BUTARIN 1935b). BUTARIN decided that the chromosome complements of arkhar and fat-tailed sheep lacked differences capable of inducing sterility in their hybrids (op. cit.:80), and later attempts to cross arkhar and merinos were based on this conclusion. Subsequently, the chromosome number in domestic sheep ($2n = 54$) was accurately established by numerous workers.

Reports of the chromosomes of wild sheep are derived largely from specimens in zoological parks where data pertinent to locality and identification are often unreported or uncertain; they include the following taxa: *O. orientalis*, $2n = 54$ (MANNA and TOLUKDAR 1965; the identification of the zoo specimen as *O. orientalis* is doubtful in view of its supposed origin from India, where the form does not exist); *O. a. musimon*, $2n = 54$, NF = 60; *O. a. cycloceros*, $2n = 58$, NF = 60; *O. a. nigri-montana*, $2n = 56$, NF = 60; *O. a. laristanica*,

$2n = 54$, $NF = 60$ (SCHMITT and ULBRICH 1968); *O. v. blanfordi*, $2n = 58$, $NF = 60$ (NADLER and LAY, MS); *O. canadensis*, $2n = 54$, $NF = 60$ (WURSTER and BENIRSCHKE 1968); *O. dalli*, $2n = 54$, $NF = 60$ (NADLER 1971). These data cast doubt on the concept of a single polytypical species of *Ovis* including all forms from *musimon* to *ammon* (TSALKIN 1951; HEPTNER et al. 1961; HALTENORTH 1963).

Further clarification of the systematic status of the various taxa of *Ovis* came from chromosomal studies of natural populations of wild sheep. In Iran urial sheep from the northeast displayed $2n = 58$, whereas in the central Elburz Mountains there was cytological and morphological evidence of intergradation between $2n = 54$ Armenian (= mouflon) sheep of northwestern and $2n = 58$ urials of northeastern Iran; the intergrade zone contains animals with $2n = 54, 55, 56, 57$ and 58 (NADLER et al. 1971). In 1971, KOROBITSINA, SAPOZHNIKOV and GORELOV investigated the chromosomes of wild sheep in southern Turkmeniya and southeastern Tadzhikistan; the joint Soviet — American Expedition to the Altai Mountains obtained chromosomes of an argali sheep, and those of a second, from the Mongolian Altai, were received (NADLER and LAY, MS).

The present paper, containing data collected independently and jointly by American and Soviet workers reports the chromosomes of wild sheep from new localities and applies these data to an evaluation of sheep evolution and systematics.

Materials and Methods

In view of the extremely confusing taxonomy of wild sheep, we prefer to utilize names at the lowest taxonomic level of the genus *Ovis* in order to identify the taxa we have examined. Chromosomes of 56 specimens of the following nine wild taxa have been studied, four forms being reported here for the first time. Two new breeds of domestic sheep are also reported.

1. *gmelinii* Blyth (1841). Type locality, eastern Turkey, vicinity of Erzerum (= Erzurum). Specimens (2 ♀♀, 3 ♂♂) from northwest Iran near the boundaries of the U. S. S. R., Marakan Protected Region ($38^{\circ} 53'$ N. latitude; $45^{\circ} 11'$ E. longitude) are quite representative of this form (NADLER et al. 1971).

2. *gmelinii* Blyth (1841) or *orientalis* Gmelin, 1774. It is not clear to which of these very similar taxa specimens (2 ♀♀, 7 ♂♂) from 20—40 km N and NE of Bijar ($36^{\circ} 06'$ N. latitude; $47^{\circ} 40'$ E. longitude) should be referred (NADLER et al. 1971). It should be noted that, following NASONOV (1923), all subsequent authors indicate the eastern Elburz as the type locality of *orientalis*. Study of the original description (GMELIN 1774) suggests that actually the type locality of *orientalis* is near Rasht, Ghilan province, i. e., in the western Elburz (we are indebted to Dr. DOUGLAS M. LAY for this interpretation).

3. *urmiana* Guenther, 1900; specimens (3 ♀♀, 4 ♂♂) from the type locality, Koyun-Daghi island in Lake Urmiah (= Rezaieyeh) ($37^{\circ} 28'$ N. latitude; $45^{\circ} 37'$ E. longitude) were studied (NADLER et al. 1971).

4. *isphaganica* Nasonov, 1910. Type locality, vicinity of Isfahan in southwestern Iran. Specimens (5 ♀♀, 3 ♂♂) from the vicinity of Murche Khort, 140 km NW of Isfahan ($33^{\circ} 38'$ N. latitude; $50^{\circ} 46'$ E. longitude) are from near the type locality.

5. *erskinei* Lydekker (1904). Sheep in the central Elburz are usually referred either to *orientalis* Gmelin, which is incorrect (see above), or to *erskinei* Lydekker, type locality — Elburz, probably the central part. NASONOV (1911, 1923) stated that two different species, *Ovis gmelinii erskinei* and *Ovis orientalis*, lived in sympatric association within the Elburz region. TSALKIN (1951) synonymized the forms *erskinei* and *orientalis*, but noted that the Elburz form exhibited mixed features. HEPTNER et al. (1961) emphasized that the existence of *orientalis* as an independent form in the Elburz was highly doubtful, and thought that in the region where the ranges of mouflon and urial come together a hybrid population existed. Specimens (1 ♀, 7 ♂♂; $2n = 54, 55$) from the Imperial Reserve just east of Tehran ($35^{\circ} 41'$ N. latitude; $51^{\circ} 34'$ E. longitude); and (3 ♀♀, 3 ♂♂; $2n = 56, 57, 58$) from the Parvar Protected Region, 50 km N of Semnan ($36^{\circ} 06'$ N. latitude, $53^{\circ} 35'$ E. longitude) represent localities inhabited by this polymorphic population of hybrid wild sheep (NADLER et al. 1971).

6. *dolgopolovi* Nasonov, 1913. Type locality, Shahrud mountains in the vicinity of Astrabad (now Gorgan). One male from the Kosh Yeilagh Protected Region, 50 km ENE of Shahrud

in the eastern Elburz is in turn 50—100 km E. of the type locality (NADLER et al. 1971). Wild sheep (1 ♀, 5 ♂♂) have also been studied from the extreme eastern Elburz, in the transition zone between the Elburz and Turkmenian and Khorasan (= Khurasan) mountains (Mohammad Reza Shah Wildlife Park, 37° 20' N. latitude; 56° 07' E. longitude) (NADLER et al. 1971). These specimens were collected 125—175 km ENE of the type locality of *dolgopolovi*.

7. *varenzovi* Satunin, 1905. Type locality, Kopet Dag Mountains (central?). One male studied from the Gezgyadik (= Gyaz'gyadik) range near Akar-Chesme (35° 54' N. latitude; 61° 21' E. longitude) in the Badkhez Reserve in southern Turkmeniya near in the junction of the boundaries of USSR, Iran and Afghanistan. This place in the southeastern Kopet-Dagh is distant from the type locality of *varenzovi* but closer to it than to the type locality of *cycloceros* (vicinity of Kandahar, southeastern Afghanistan).

8. *bochariensis* Nasonov, 1914. Type locality, vicinity of Bal'dzhuan on the southeastern slopes of the Vakhshskii mountains (between the Vakhsh and Kizilsu rivers). The chromosomes of 1 ♀ and 2 ♂♂ from southwestern Tadzhikistan have been studied: 1 ♀ and 1 ♂ from the Pyandzh Kara-Tau range (37°—38° N. latitude; 69°—70° E. longitude) and 1 ♂ born in the Dushanbe Zoological Park from parents wild-caught in the Pyandzh Kara-Tau range (father) and the Sar-Sorak range (38°—39° N. latitude; 69°—70° E. longitude). All these animals are in the Dushanbe Zoological Park, but the localities where they were wild-caught are known exactly inasmuch as Sapozhnikov captured and delivered them to the Zoological Park.

9. *przevalskii* Nasonov, 1923. The type locality of the true argali — *O. ammon* Linnaeus (1758) — is Semipalatinsk in the Altai Mountains, whereas the closely similar form *przevalskii* has been described from the Sailyugem Mountains on the USSR — Mongolian border. One male was studied; from the Gorno-Altai Autonomous District, northeast of the Chuiskaya steppe, in the Taldu-Air, the western spurs of the Chikhachev mountains (50° 03' N. latitude; 89° 25' E. longitude), 30 km N. of Tashanta (= Tashakta) along the Chuiskaya highway. This point is 30 km N of the eastern end of the Sailyugem range, the type locality for *przevalskii*. A second male, probably referable to *przevalskii*, was collected in the Mongolian Altai (46° 30' N. latitude; 93° 00' E. longitude) (NADLER and LAY, MS).

In addition, the chromosome complements of the following forms of domestic sheep have been studied:

10. Karakul sheep: 1 ♂ from the State farm Chemen-Abid, Takhta-Bazar region, Turkmen S. S. R.

11. Fat-tailed sheep: 2 ♀♀ from Tehran, Iran.

Chromosomes were analyzed from marrow cell suspensions cultured in vitro for 8 hours with colcemide (NADLER et al. 1971), by short-term leucocyte culture, or by analysis of skin biopsies grown in tissue culture by Dr. T. C. Hsu. Karyotypes were constructed from enlarged photomicrographs.



Fig. 1. Karyotype of male Asiatic mouflon (*Ovis orientalis isphaganica*) from Murche Khort, southwestern Iran (2n=54)

Results

All specimens of *isphaganica* had a $2n = 54$ and karyotypes containing six large metacentric and 46 acrocentric autosomes; a large acrocentric X and a small biarmed Y chromosome (Fig. 1). The $2n$ of *varenzovi* from the Kopet Dag mountains and of *bochariensis* from Tadzhikistan was 58 (Fig. 2). The karyotype contained two large metacentric and 54 medium to small-sized acrocentric autosomes; the X was a large acrocentric and the Y a small biarmed chromosome. The form *przevalskii*

Fig. 2a. Karyotype of a male urial (*Ovis vignei dolgopolovi*) from Kosh Yeilagh, northeastern Iran ($2n = 58$)

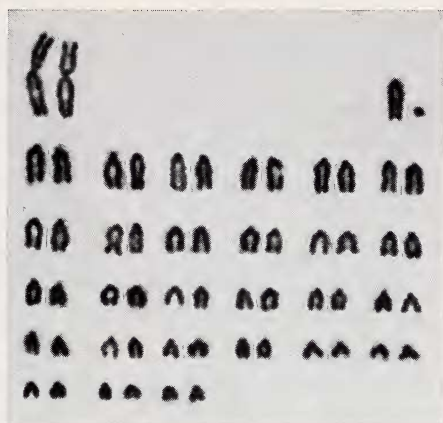


Fig. 2b. Karyotype of a male urial (*Ovis vignei varenzovi*) from the Badkhez Reserve, southern Turkmeniya ($2n = 58$)

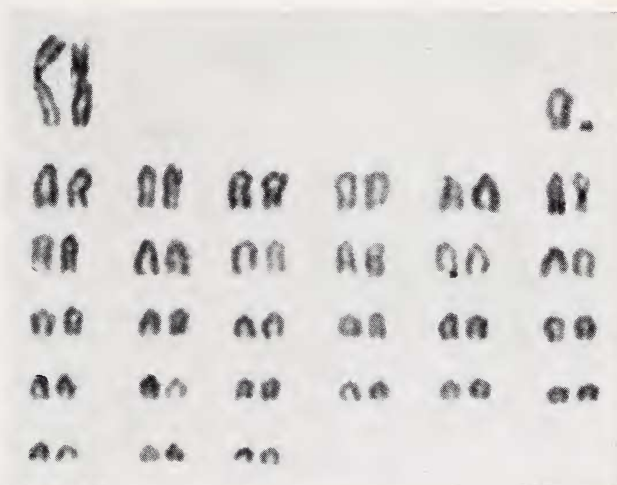


Fig. 2c. Karyotype of a male urial (*Ovis vignei bochariensis*) from southwestern Tadjikistan ($2n = 58$)

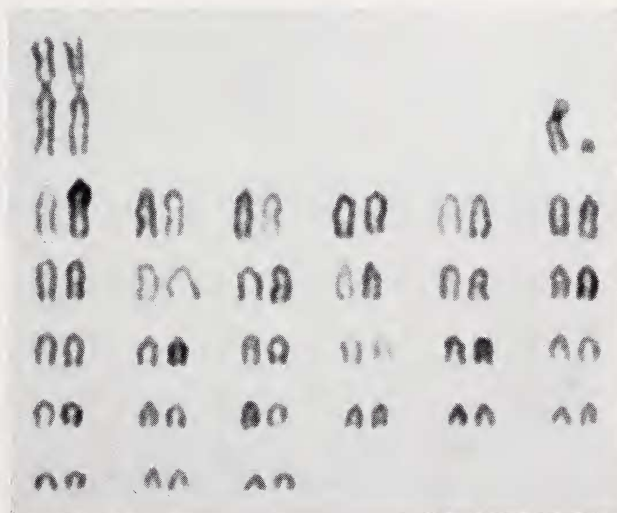




Fig. 3a. Karyotype of a male argali (*Ovis ammon przewalskii*) from Gorno-Altai Auton. Dist., USSR ($2n = 56$)

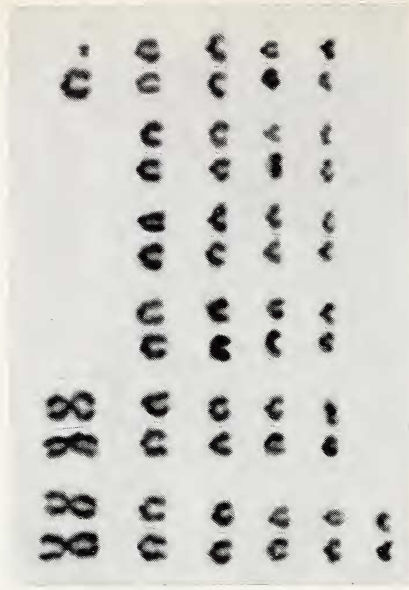


Fig. 3b. Karyotype of a male argali (*Ovis ammon przewalskii*?) from the Altai mountains, Mongolian People's Republic ($2n = 56$)

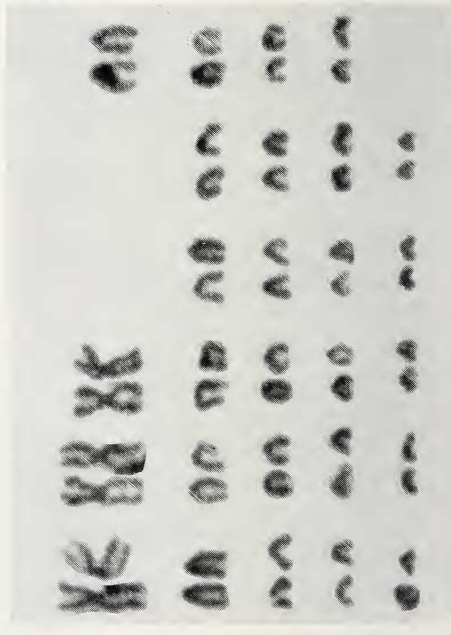


Fig. 4a. Karyotype of a female Karakul sheep (*Ovis aries*) from Kushka, southern Turkmeniya ($2n = 54$)



Fig. 4b. Karyotype of a female fat-tailed sheep (*Ovis aries*) from Teheran, Iran ($2n = 54$)

from the Gorno-Altai of the Soviet Union and the Mongolian Altai mountains had a $2n = 56$, the karyotype consisting of four large metacentric and 52 medium to small-sized autosomes; a large acrocentric X and a small biarmed Y chromosome (Fig. 3). Both the fat-tailed and Karakul breeds of domestic sheep possessed a $2n = 54$ and similar karyotypes that contained six large metacentric and 46 medium to small-sized autosomes; a large acrocentric X and a small biarmed Y chromosome (Fig. 4).

The karyotypes of wild sheep from the Kopet Dag and Tadzhikistan are indistinguishable from *dolgopolovi* described by NADLER et al. (1971) from northeastern Iran, and *cycloceros*, supposedly from Afghanistan (SCHMIDT and ULBRICH 1968). Similarly, the $2n = 56$ chromosome complement of *przevalskii* from the Altai mountains is similar to that of *nigrimontana*, presumably from the Kara-Tau (SCHMITT and ULBRICH 1968), and to the $2n = 54 \times 2n = 58$ hybrids (*erskinei*) possessing $2n = 56$ that occur in the central Elburz Mountains of Iran (NADLER et al. 1971).

Finally, the chromosomes of both breeds of domestic sheep and of wild *isphagana* were similar to those of domestic sheep previously reported (see WURSTER and BENIRSCHKE 1968); to *gmelinii*, *urmiana* and *orientalis* from northwestern Iran; to *laristanica*, supposedly from southern Iran; and to *musimon* from the Mediterranean region (SCHMITT and ULBRICH 1968; NADLER et al. 1971).

Discussion

Taxonomic Conclusions

Large amounts of cytogenetic data on wild sheep are difficult to obtain. In spite of the small numbers of specimens available from most places, a distinctive geographic pattern seems to be emerging which corresponds rather well with the grouping of the various named forms of wild sheep proposed by SOKOLOV (1959), PFEFFER (1967) and GEIST (1971a). The present material enables us to name four groups of wild sheep, while at the same time recognizing that the nomenclatorial designations are provisional, until more detailed biosystematic studies of the genus are completed.

*Group I. Eurasian $2n = 54$ chromosome sheep — European mouflon (*Ovis musimon*) and Asiatic mouflon (*Ovis orientalis*)*

Mouflon sheep of the western Palearctic, from the Mediterranean to northwestern and southern Iran, are usually characterized by ringed but not ridged horns, twisted either supracervically (heteronymous) with convergent tips (Asiatic or Armenian mouflon), or by "normal" (homonymous) twisting with divergent tips (Mediterranean or European mouflon). The throat ruff is black; in some forms a white "saddle patch" is present, and the small rump patch is sharply defined. Body size is small, but with relatively long legs and broad tail.

*Group II. Eurasian $2n = 58$ chromosome sheep — urial (*Ovis vignei*)*

Urial sheep of Middle Asia, from northeastern Iran to Tadzhikistan and Afghanistan (and probably extending into northwestern India) usually possess "normal" horns with divergent tips, which are ridged as well as ringed or keeled. The throat ruff is white, and the small rump patch is poorly defined. Body size is intermediate, with relatively long legs, and a thin, light tail. Where the two types (mouflon and urial) meet in northcentral Iran, a narrow hybrid zone is formed, with sheep there having mostly "intermediate" horn form (sicklelike horns growing in one plane,

with the tips pointing toward the neck, rather than above, as in most Asiatic mouflons or below, as in most urials). Hybrids also possess a mixed, black-and-white throat ruff.

*Group III. Eurasian $2n = 56$ chromosome sheep —arkhar or argali (*Ovis ammon*)*

Arkhar/argali sheep of Central Asia inhabit the Pamirs, Tyan Shan, and Altai mountains, and extend eastward through Tibet and Mongolia to China. They are characterized by normally twisting (homonymous) horns, often very long and/or massive, and often with widely divergent tips (as in *polii*), which are ringed, but not usually keeled. Body size is large, with long legs, a large, diffuse rump patch, and thin, light tail. In northern argali populations (Pamir, Tyan Shan, Altai) the throat ruff is scanty or absent, but at least some southern argalis (Tibet, China) have a well-developed white throat ruff.

*Group IV. Amphiberingian (eastern Eurasian and western North American) $2n = 54$ chromosome (as far as known) sheep — snow sheep (*Ovis nivicola*), thinhorn or Dall sheep (*Ovis dalli*) and bighorn sheep (*Ovis canadensis*)*

These sheep are often placed in a separate subgenus, *Pachyceros*, characterized by a wide skull with relatively short facial region, and shallow lacrymal pit, with which is associated a vertical, half-moon shaped preorbital gland, in contrast to the slit-like horizontal preorbital gland found in the subgenus *Ovis*. Body size is moderate to large, stocky with relatively short legs. The rump patch is well-defined, and the tail broad and dark (except in *O. dalli*); there is no throat ruff. Horns are normally twisted, and moderately heavy to massive, with a well-developed lateral keel.

Future studies must determine possible range overlap between urial and mouflon sheep in southern Iran and between urial and arkhar/argali sheep in Ishkashim, southern Tadzhikistan and in Ladakh. Possible homologies between $2n = 54$ chromosome domestic and Eurasian wild sheep (*musimon*, *orientalis*) and American wild sheep (*canadensis*, *dalli*) warrant further cytogenetic and breeding studies. The origin of North American sheep cannot be determined without chromosomal studies of *O. nivicola* including the isolated population on the Putoran plateau, *O. n. borealis* (NASONOV 1923; MICHURIN and MIRONENKO 1966).

On the basis of cytogenetic data we believe that urial sheep ($2n = 58$) may be the most primitive. Robertsonian centric fusion is a cytological event frequently observed in both wild and domestic Bovoidae (see WURSTER and BENIRSCHKE 1968; GUSTAVSSON 1969). Considerable direct and indirect evidence suggests that fusion rather than fission is the predominant mechanism for changes in diploid number in cattle, sheep and goats, and it seems probable that the $2n = 58$ of urial sheep is most representative of the ancestral sheep chromosome complement and that the sheep with $2n = 56$ and $2n = 54$ karyotypes evolved from the former. This view is consistent with GEIST's (1971a) hypothesis, based on behavioral and morphological data, that the Barbary sheep (*Ammotragus lervia*) with $2n = 58$, may have been ancestral to true sheep (*Ovis*).

It is possible that the present range of urials is smaller than in the past; it is notable that the present range of $2n = 58$ urials occupies a region which did not undergo severe glacial and climatic changes during the Pleistocene. Farther west, in the Main Caucasus, certain areas of the Little Caucasus, and in the Alps, glaciation was extensive; it was through this region that $2n = 54$ chromosome mouflons must have dispersed to Corsica and Sardinia, and such mouflons or their ancestors lived or now live there. Similar strong glaciation occurred in the higher mountains of the

Karakoram, Pamirs, Tibetan periphery, Tyan-Shan, and southern Siberia, where $2n = 56$ chromosome arkhar/argali sheep now live. We think that evolution of the sheep in the regions west of Iran and Afghanistan was in the direction of decreasing size, becoming mouflon-like and developing into a $2n = 54$ chromosome form, whereas in the east, in the high mountains of Central Asia and southern Siberia, sheep evolved larger body and horn size of the arkhar/argali with $2n = 56$ chromosomes. The evolution of larger body size, and in particular, very large horns, in arkhar/argali and in amphiberian sheep dispersing into formerly glaciated areas is discussed by GEIST (1971b).

There are several alternative explanations for this geographic pattern. First, ancestral sheep with $2n = 58$ originating in Middle Asia (northeastern Iran, Turkmeniya, Tadzhikistan, Afghanistan, Pakistan) may have developed a polymorphism that included animals with $2n = 58, 57, 56, 55$ and 54 . Subsequently, sheep with successively lower diploid numbers ($2n = 56-54$) spread both westward toward the Mediterranean and eastward into Mongolia, eastern Siberia and thence to North America. A second explanation postulates development of $2n = 56$ and 54 karyotypes from different geographic isolates of the ancestral $2n = 58$ population. Based on the latter hypothesis we predict that a $2n = 56$ will predominate in populations of argali throughout their distribution, and that *O. nivicola* will be characterized by either $2n = 56$ or more probably $2n = 54$ since it is regarded as more similar to North American sheep (CAERNYAVSKII 1962).

Recently, GEIST has, on the basis of independent behavioral evidence, also postulated that urial sheep are primitive. He suggests that mouflons and amphiberian sheep ($2n = 54$) are both derived from urials in an early radiation of *Ovis*, and that arkhar/argali ($2n = 56$) are more recently evolved from urial stock (1971a; pers. comm.). We tend, instead, to agree with GROMOVA (1936), who considered mouflon sheep to be quite recent forms. Fragmentary paleontological data are very interesting in demonstrating that during the Middle Pleistocene large sheep, very different from later mouflons, lived in the Main Caucasus, Transcaucasus (Binagadi) and the mountains of Crimea (GROMOVA 1935; VERESHCHAGIN 1959), and are perhaps evidence of a more extensive distribution of $2n = 58$ urial ancestors of the present *Ovis*; HERRE and KESPER (1953) believed that larger mid-Pleistocene sheep gave rise to smaller mouflon-like sheep in Europe. Additionally, "mouflon" are reported from North Africa during the Pleistocene (KURTÉN 1968), but insufficient information is presented to ascertain whether these might also have differed from modern $2n = 54$ mouflon. On the other hand, our concept of the evolution of amphiberian snow, thinhorn and bighorn sheep in eastern Siberia and North America does not contradict the view of COWAN (1940), or STOCK and STOKES (1969) based on fossil cranial and horn morphology, or of GEIST (1971a), based on behavioral data.

Geographical Distribution

There is no adequate map of the distribution of wild sheep in the Holarctic, although the distributions of *O. dalli* and *O. canadensis* have been accurately mapped in North America (HALL and KELSON 1959). Comparatively satisfactory information on the recent distribution of snow sheep is given in SOKOLOV's review (1959) and in other recent studies (PORENKO et al. 1963; EGOROV 1965). We have summary maps of the distribution of wild sheep in the USSR (BOBRINSKII et al. 1944, 1965) or portions thereof (AFANAS'EV et al. 1953). The range of wild sheep in Asia south of the USSR has scarcely been studied and even TSALKIN's fundamental work has no map of the geographical distribution of sheep; the only available map (PFEFFER 1967) is too schematic.

TSALKIN's monograph (1951) contains many known localities for wild sheep. Unfortunately, they are very difficult to map because of frequent changes in, and confusing transcription of, place names. In addition to the above, the following sources were used to compile Figure 5: ELLERMAN and MORRISON-SCOTT (1951) (general); PFEFFER (1967) (*musimon* in the Mediterranean); HALL (1966) (*anatolica* in central Turkey); SARKISOV (1941, 1944); RADDE (1899); VERESHCHAGIN (1959) (*gmelinii* in eastern Turkey, Transcaucasus and northwestern Iran); BURRARD (1925) (*hodgsonii* in Tibet) NADLER and LAY's unpublished data were also included in circumscribing the range of Iranian sheep. The unpublished observations of N. N. VORONTSOV, G. N. SAPOZHNIKOV and K. V. KOROBITSINA were utilized in defining the range of sheep in Middle Asia, Kazakhstan and southern Siberia. Distribution of sheep in Central Asia is based on BANNIKOV (1954) and on ALLEN's data (1940) which, while good, are poorly mapped; the reports of Russian expeditions in Central Asia (PEVTSOV 1879; ROBOROVSKI 1900; KOZLOV 1905) were also employed.

We regard this map (Fig. 5) as a first approximation to the original Holocene distribution of wild sheep. What is most significant is that the range of sheep in southern Asia at present and in the recent past consists of a series of "rings". Temporal disjunctions between these rings, and consequent weakening or interruption of gene flow has stimulated divergence of various populations.

Distribution of Mouflon Sheep

The connection of Corsica and Sardinia with Europe dates back to the Middle Pleistocene (FURON 1959); possibly it was then that mouflons spread to these islands. The Pleistocene range of sheep in the Main and Little Caucasus formed part of a ring connecting the present range of *gmelinii* with that of *anatolica*; the connections seem to have been lost only in the past few centuries.

The series *gmelinii-isphaganica-laristanica* constitutes the western half of the Iranian distribution ring, encircling the Dasht-I-Lut and Dasht-I-Kavir deserts. Discovery of the hybrid zone between $2n = 54$ and $2n = 58$ chromosome sheep in the Elburz Mountains suggests that in northern Iran this ring has long been incomplete and was probably joined in the Holocene, perhaps as a result of the wasting of glaciers in central Elburz.

Distribution of Urial Sheep

The eastern part of the Iranian ring of sheep, which connects the Turkmeniyani-Khorassan mountains (*dolgopolovi*, *varenzovi*) and north Afghan portion of that range with Laristan (*laristanica*) and Baluchistan, passes (or previously did) to the east of the Dasht-I-Lut desert along the Ezdegerd, Kalat, Gamshadzai, Bageran (= Bagiran) and Palangan mountains and the Sepkheg plateau. In Afghanistan the sheep range borders the Dasht-I-Margo and Registan deserts, to the north of which lives typical *cycloceros* in the mountainous regions of northeastern Afghanistan (Khazardzat, Kohistan, Nuristan). To the southwest *blanfordi* ranges; forms intermediate between *cycloceros* and *varenzovi* are farther north. Somewhere along these north-south trending mountains a zone of potential contact between ranges of $2n = 54$ and $2n = 58$ chromosome sheep may exist. Of great interest is the report by HARRISON (1968) of a urial-type sheep from the mountains of Oman on the Arabian peninsula opposite Laristan and Baluchistan. This relict distribution may represent a urial population which had a wider distribution in the most recent glacial period, and became isolated with rising sea level in the Persian Gulf at the end of the Würm-Wisconsin (see above).

The range of the steppe form, *arkal*, diverges from that of Kopet Dagh *varenzovi*, through the Little and Great Balkhan across the Krasnovodsk plateau northward to the Mangishlak peninsula. Quite recently sheep were distributed through the mountains

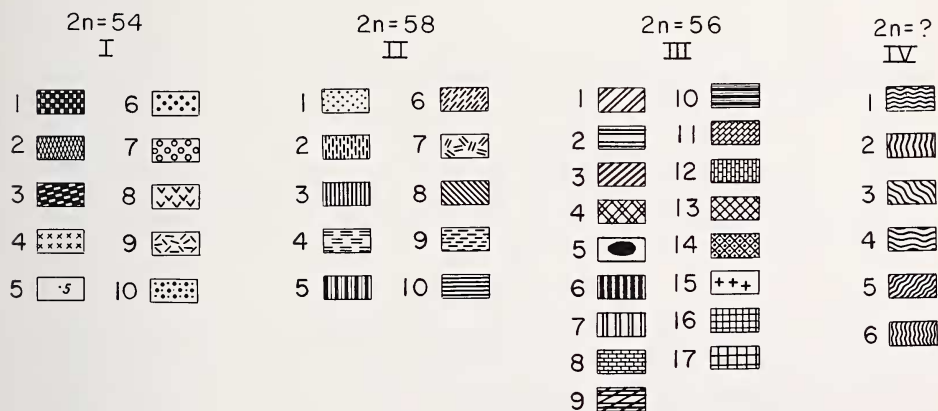


Fig. 5. Map of the distribution of wild sheep in the Old World. — I. Distribution of mouflon sheep ($2n = 54$): 1—0. *m. musimon*; 2—0. *m?* *ophion*; 3—0. *orientalis anatolica*; 4—0. *o. gmelinii*; 5—0. *o. urmiana*; 6—0. *o. orientalis*; 7—0. *isphaganica*; 8—0. *o. laristanica*; 9—0. *ssp?* 10—hybrid zone. — II. Distribution of urial sheep ($2n = 58$): 1—0. *vignei dolgopolo*; 2—0. *v. varenzovi*; 3—0. *v. arkal*; 4—0. *v. cycloceros*; 5—0. *v. blanfordi*; 6—0. *v. punjabiensis*; 7—0. *v. vignei*; 8—0. *v. bochariensis*; 9—0. *v?* *severtzori*; 10—0. *ssp?* — III. Distribution of arkhar/argali sheep ($2n = 56$): 1—0. *ammon hodgsonii*; 2—0. *a. poili*; 3—0. *dalai-lamae*; 4—0. *a. darwini*; 5—0. *a. kozlovi*; 6—0. *a. intermedia*; 7—0. *a. karelini*; 8—0. *a. nigrimontana*; 9—0. *a. collum*; 10—0. *a. sairensis*; 11—0. *a. littledalei*; 12—0. *a. ammon*; 13—0. *a. przewalskii*; 14—0. *a. mongolica*; 15—0. *a. dauricus*; 16—0. *a. jubata*; 17—0. *a. ssp?* — IV. Distribution of snow sheep ($2n = ?$): 1—0. *n. nivicola borealis*; 2—0. *n. potanini*; 3—0. *n. alleni*; 4—0. *n. lydekkeri*; 5—0. *n. nivicola borealis*; 6—0. *n. ssp?*

of the northwestern Kara-Kum (Chelyungkri plateau, Kaplakir, Karabaur); it is possible that in the region of the southeastern Ust-Urt chink (= arroyo), near the delta of the Amu-Darya, the range of *arkal* almost merged with the range of *severtzovi*, which extended westward from the mountains of the central Kizil-Kum, and may have reached Sultanizdag (north of Biruni).

The range of *vignei* includes Ishkashim, Little Tibet and, perhaps, Ladakh, merging on the west with *cycloceros*. To the south of the region inhabited by *vignei*, the form *punjabiensis* now lives, throughout Kashmir and the Potwar plateau. Sheep also penetrated into the region of the Sulaiman mountains, from the east encircling the valley between the Kabul and Indus rivers and from the west, through Waziristan.

The ranges of *vignei* and *bochariensis* in western Tadzhikistan are connected by a narrow mountainous strip through Badakhshan (in Afghanistan) and the Khazratishakh ridge. The range of the latter form is connected with the mountainous central Kizil-Kum (Kul'dzhuktau, Tamditau, Bukantau and others), inhabited by *severtzovi*, through the Nuratau range. Parenthetically, it should be noted that the placement of *severtzovi* in the urial group, as done by TSALKIN (1951) and SOKOLOV (1959) is somewhat uncertain, and other authors consider it to be an arkhar/argali (NASONOV 1911; ELLERMAN and MORRISON-SCOTT 1951; CLARK 1964; CARRUTHERS 1949).

Distribution of Arkhar/Argali Sheep

The Ishkashim region in Tadzhikistan is inhabited by small urial sheep whose range meets and may even overlap the range of large arkhar/argali sheep. (This zone of potential overlap is discussed in greater detail in VORONTSOV et al. 1972b). The range of the latter is also composed of a series of ring and half-ring distributions. The wild sheep of the Tibetan Plateau are southern argalis, *hodgsonii* (ENGELMANN 1938); they meet the ranges of *darwini* on the northeast, *dalai-lamae* on the north, and perhaps *polii* on the northwest and west. The range of *polii* and of *hodgsonii* overlap or contact with the range of *vignei* (BURRARD 1925; KINLOCH 1892). In the north the range of *polii* merges with the range of the Tvan-Shan race *karelini*; the latter encircles Kashgariya to the north, meeting the range of *darwini*, which in turn merges with *kozlovi* in the Yabaraï and Beishan mountains. To the west, the form *karelini* intergrades with *nigrimontana* of the low-lying Kara-Tau mountains of Kazakhstan. The range of *karelini* also joins that of *collium*, which inhabits the hills of Kazakhstan, through the Chu-Iliiskii mountains. Encircling the Lake Balkhash region from the south, the range of *karelini* comes close to contact with the range of *littledalei* in the Dzhungarskii Ala Tau, and the latter form in turn approaches *sairensis* of the Saur Mountains through the Barlik and Dzhair (= Chierh) ranges. The range of *sairensis* joins that of *collium* in the Tarbagatai Mountains, thus closing the distribution ring around Lake Balkhash from the north, while at the same time bordering the Zaisan depression on the south. In the Kalbinskii Altai, the range of *collium* reaches that of *ammon* (s. str.) of the southwestern Altai and the range of *ammon* in turn meets that of *przevalskii* inhabiting the Sailyugem Mountains and the Mongolian Altai. This portion of the range surrounds Dzhungariya on the north and the depression of the northwestern Mongolian lake region on the southwest. Further east in the Altai and western Sayan mountains, *ammon*, or *przevalskii* merges, across the Tannu-Ola Mountains, with the range of the southern form *mongolica* in the Khangai (= Hangay) mountains.

As late as the 18th century argali sheep lived in Selengan Dauriya and the mountains adjacent to the Ononskaya steppe, and thus probably formed a continuous wild sheep range from the Sayan Mountains through Transbaikaliya, and joined the range of *mongolica* of the Khangai (= Hangai) via the Khentai (= Henteyn) moun-

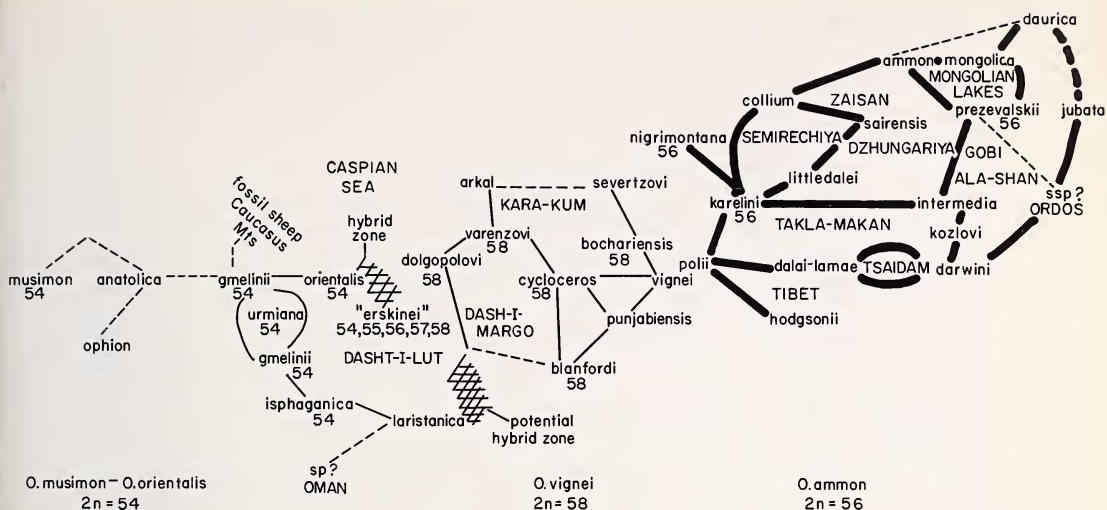


Fig. 6. Schematic distribution of wild sheep in southern Eurasia showing inter-linked rings and half-rings of populations (hybrid zones indicated by cross-hatching)

tains (HEPTNER et al. 1961). Finally, it is possible to interpret the remains of sheep in eastern Transbaikaliya (*dauricus*) as evidence of former connection between the range of the southern argali, *jubata*, of the Great Khingan (= Hingan) mountains and the historical range of argali sheep in western Transbaikaliya. It should also be noted that sheep are distributed in the Central Asian mountains bordering the Kashgariyan, Tsaidam, Ala-Shan and Gobi deserts, and probably link the southern and northern populations of argalis.

Thus, the total distribution area of wild sheep in the southern Palearctic has an interconnected structure consisting of multiple interlinked rings and half-rings (Fig. 6), in this respect resembling the well-known case of *Larus argentatus-cachinnans-fuscus* (STRESEMANN and TIMOFEEV-RESSOVSKY 1947; TIMOFEEV-RESSOVSKY and STRESEMANN 1959). Past breaks in the links of the rings and their periodic restoration resulted in intensive differentiation between populations. According to KOLMOGOROV (1935), it is precisely such a semi-isolated structure of the distribution of a species which results in high rates of evolution.

Domestication of Sheep

Question concerning the origins of domesticated sheep may also be reevaluated using chromosomal data. REED (1960) and PERKINS (1964) both believed that archeological evidence pointed to Asiatic mouflons as the ancestors of domestic sheep. On the other hand, ZEUNER (1963) suggested that wild urials from the Aralo-Caspian basin were first domesticated and that they later spread throughout the Middle East and to Europe; a second group of sheep originated from mouflon stock ($2n = 54$) and then spread to Europe, thus intermingling with the stock derived from urials. Farther east in India, Tibet and eastern Asia, domestic sheep were believed to have evolved primarily from urial ($2n = 58$) stock with some admixture of arkhar/argali ($2n = 56$) genes.

Karyotypes are identical ($2n = 54$) in all breeds of domestic sheep, and in subspecies of wild sheep of the mouflon type (*musimon*, *gmelinii*, *urmiana*, *orientalis*, *isphaganica*, *laristanica*) thus far studied. Their karyotypes markedly differ from those of urial sheep (*dolgopolovi*, *varenzovi*, *bochariensis*, *cycloceros*) ($2n = 58$) as

well as from the arkhar/argali sheep (*przevalskii*, *nigrimontana*) ($2n = 56$). Taken together, this supports the REED-PERKINS hypothesis that sheep domestication proceeded to the west of a line extending from the Caspian to the Gulf of Oman and that urial and arkhar/argali sheep should not be considered among the ancestors of domestic sheep. Modern archeological data show that the domestication of sheep preceded that of the other hooved animals, possibly even goats, with the earliest findings of domestic sheep in the Near East dating back to the ninth millenium B. C. (TSALKIN 1968; REED 1969). This conclusion is also supported by a comparison of transferrins which showed greater similarities between domestic sheep and wild sheep ($2n = 54$) from northwestern Iran (LAY et al. 1971).

It is known that the cultures of the nomads of Central and Middle Asia and Kazakhstan relied primarily upon sheep and horse breeding. Previously, BENIRSCHKE and co-workers (1965, 1967) demonstrated that the wild *Przhevalskii's* horse, *Equus przewalskii*, has $2n = 66$ whereas the domestic horse, *E. caballus* has $2n = 64$. The data available (SOKOLOV 1959; HEPTNER et al. 1961) seem to indicate extensive hybridization between the wild horse (tarpan, *E. caballus gmelini* Antonius) of the southern Russian steppes and domestic horses. This suggests the possibility of karyotypic similarity between the domestic horse and tarpan, and many authors following GROMOVA (1949), recognize two species of wild horses. Implicit from these data is the interpretation that horse domestication occurred west of the Ural river.

Thus, judging from cytogenetic data, sheep domestication may have taken place in the regions north and northeast of the Mediterranean and/or in the Near East, while that of horses occurred in the steppes of eastern Europe. Sheep and horse breeding was a secondary event in the cultures of Kazakhstan, Middle Asia and Central Asia, whose nomadic life was, however, closely connected with breeding of these animals. The introduction of sheep breeding into Middle Asia dates as far back as the fifth-sixth millenia B. C. (southern Turkmeniya, Dzheiton culture, Chagillidepe settlement in Kopet Dag, radiocarbon date 5036 ± 100 years B. C., TSALKIN 1970a, 1970b), i. e., at least three-four thousand years after the domestication of this species in the Near East (PERKINS 1964; TSALKIN 1970b).

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Summary

Old World wild sheep may be divided into four groups, with different diploid chromosome numbers and morphological characters. There are, from west to east, mouflon ($2n = 54$) in the Mediterranean region and the Near East; urial ($2n = 58$) in Middle Asia from eastern Iran to Tadzhikistan and probably West Pakistan; arkhar/argali ($2n = 56$) in Middle and Central Asia; and snow sheep ($2n = ?$) (subgenus *Pachyceros*) in eastern Siberia. The systematic status of sheep from Europe to Central Asia (subgenus *Ovis*) remains uncertain; in this broad area

wild sheep are distributed in interconnected rings many of which have been repeatedly broken and rejoined during the Pleistocene, leading to differentiation of isolates and subsequent introgression. Domestic breeds of sheep so far studied all appear to be derived from a mouflon ($2n = 54$) ancestor in the Near East.

Zusammenfassung

Cytogenetische Differenzierung, geographische Verbreitung und Domestikation paläarktischer Schafe (Ovis)

Die Altweltschafe können in vier Gruppen mit unterschiedlichen diploiden Chromosomenzahlen und morphologischen Merkmalen untergliedert werden: Von Westen nach Osten Mufflon ($2n = 54$) in der Mittelmeerregion und im Nahen Osten; Urial ($2n = 58$) in Mittelasien vom östlichen Iran bis Tadzhikistan und wahrscheinlich Westpakistan; Argali/Arkar ($2n = 56$) in Mittel- und Zentral-Asien; Schneeschaf ($2n = ?$) (Subgenus *Pachyceros*) in Ostsibirien. Der systematische Status der Schafe von Europa bis Zentralasien (Subgenus *Ovis*) bleibt ungewiß; in diesem großen Areal sind die Wildschafe in untereinander verbundenen Ringen verbreitet, von denen viele mehrfach in Pleistozän unterbrochen und wieder verbunden wurden, das führte zur Bildung von Isolat und nachfolgender Introgression. Hausschafe, soweit untersucht, scheinen von einem Mufflonvorfahren ($2n = 54$) im Nahen Osten abzustammen.

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